

NEMATOCYST DISCHARGE, HISTOINCOMPATIBILITY, AND THE FORMATION OF SWEEPER TENTACLES IN THE CORAL *GALAXEA FASCICULARIS*

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ABSTRACT

The roles of nematocyst discharge of ordinary tentacles and histoincompatibility responses in the formation of sweeper tentacles in the coral *Galaxea fascicularis* were examined. Colonies of *G. fascicularis* could be divided into several groups according to whether their ordinary tentacles discharge nematocysts against each other. Polyps isolated from colonies of the same or different groups were set about 5 mm apart with tentacles touching and maintained for about five months in this position. When two polyps isolated from colonies of different groups were paired, they developed sweeper tentacles. Usually, one of the paired polyps was damaged, but in some combinations both polyps survived without damage. Polyps that did not discharge nematocysts against each other did not compete through sweeper tentacle formation. In some combinations, paired polyps showed histoincompatibility and developed tentacles at intermediate stages between ordinary and sweeper tentacles. In other combinations, paired polyps fused and developed no or only a few intermediate tentacles. The present results show that the nematocyst discharge response has a major role in eliciting formation of sweeper tentacles, but that the histoincompatibility response may also stimulate transformation of ordinary tentacles into sweeper tentacles.

INTRODUCTION

Corals compete for space in several ways. Interspecific competition through extracoelenteric digestion with mesenterial filaments (Lang, 1973), overgrowth (Porter, 1974; Connell, 1976), and sweeper tentacle formation (den Hartog, 1977; Richardson *et al.*, 1979; Wellington, 1980; Bak *et al.*, 1982; Chornesky, 1983) are well known. Although corals generally do not use mesenterial filaments in intraspecific competition for space, they compete with other conspecific colonies through cytotoxic histoincompatibility (Hildemann *et al.*, 1975, 1977a, b) and direct overgrowth (Potts, 1976, 1978; Rinkevich and Loya, 1983). *Galaxea fascicularis* uses sweeper tentacles in intraspecific competition (Hidaka and Yamazato, 1984). Sweeper tentacles are formed when corals come into contact with other colonies (Hidaka and Yamazato, 1984) or with other corals and some anthozoans (Chornesky, 1983). Sweeper tentacles have a different complement of nematocysts than ordinary tentacles (den Hartog, 1977; Hidaka and Yamazato, 1984). But there are tentacles at intermediate stages between ordinary and sweeper tentacles both in terms of nematocyst composition and external appearance (Hidaka and Yamazato, 1984). Hidaka and Yamazato (1984) suggested that ordinary tentacles transform into sweeper tentacles and that changes in nematocyst composition accompany this

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transition of tentacles. This is also the case with catch tentacles, which are similar to sweeper tentacles, and used in aggression by some sea anemone species (Purcell, 1977; Watson and Mariscal, 1983).

It is, however, not yet understood whether nematocyst discharge of ordinary feeding tentacles plays some role in intraspecific interactions. It also remains to be elucidated what kind of stimulus induces development of sweeper tentacles. Recently, Chornesky (1983) found that artificial damage or tactile stimuli cannot induce sweeper tentacle formation, though damage caused by extruded mesenterial filaments of other corals elicits sweeper tentacle formation in *Agaricia agaricites*.

The present paper first examines the roles of (1) nematocyst discharge of ordinary tentacles and (2) the histoincompatibility response in self and non-self recognition. Second, it examines whether the nematocyst discharge of ordinary tentacles or histoincompatibility response is necessary for inducing formation of sweeper tentacles. Finally, it shows that the nematocyst discharge response of ordinary tentacles plays a major role in eliciting formation of sweeper tentacles, though the histoincompatibility response may also stimulate formation of sweeper tentacles. The results also show that the histoincompatibility response is more sensitive in recognition of self and non-self than is the nematocyst discharge response.

MATERIALS AND METHODS

Colonies of *Galaxea fascicularis* were collected from the reef at Sesoko Marine Science Center, University of the Ryukyus, in Okinawa. They were maintained in tanks supplied with running sea water until used. Colonies used in this experiment could be divided into several morphs according to polyp coloration: morph 1 (BG), brown with greenish oral disk; morph 2 (Gt), brown but lateral tentacles are light green; morph 3 (Gs), brown but tentacles on the major septa are light green; morph 4 (B), entire polyp is pale brown; and morph 5 (Wt), brown with white fluorescent lateral tentacles.

Nematocyst discharge responses

Polyps with their corallites were isolated from a colony by pulling with forceps. The isolated polyps were placed in a holding tank for at least 6 h or sometimes for about 2 months to recover from the possible damage caused during the isolation process. The subject polyp was then placed in a dish filled with sea water and allowed to adapt to the experimental condition until its tentacles were extended. Lateral wall tissue of the stimulus polyp was applied to the tentacle tip (acrosphere) of the subject polyp for about one second. Then the stimulus polyp was gently removed from the tentacle tip to examine whether the tentacle tip adhered to the target tissue. When the tentacle tip adhered to the target tissue, it was assumed that it discharged nematocysts against the target tissue (as assumed in Lubbock, 1980; Ertman and Davenport, 1981). This test was repeated three times for each tentacle until the tentacle tip adhered to the target tissue, although adhesion usually occurred at the first trial. At least three tentacles of a polyp were examined for each combination of colonies. For the colony pairs used in contact experiments, the test was performed on at least nine tentacles of three polyps. The nematocyst discharge responses between nine colonies were examined and two series of such experiments were performed.

Contact experiments

Colonies of *G. fascicularis* were divided into several groups according to whether they discharged nematocysts against each other (see Results). In this experiment, polyps isolated from colonies belonging to the same group or to different groups were paired. Seven replicated pairs of polyps were made for each combination of colonies. The paired polyps were kept at a distance of about 5 mm so that the ordinary tentacles of the two polyps touched each other. Isolated polyps were held on a polyvinylchloride stage by inserting the basal skeletal portion of the polyp into a hole in the stage. The paired polyps were placed in a tank supplied with running sea water with a distance between pairs of about 10 cm. They were observed at intervals of about two weeks for up to five months. It was recorded whether the polyps had developed sweeper tentacles, whether they suffered damage from the neighboring polyp, and whether the tissues of both polyps had fused.

At the end of the contact experiment, the paired polyps were fixed in 10% formalin in sea water. Their tentacles were cut off and their nematocyst composition was examined under a microscope at a magnification of 200–400 \times . The tentacle tips (acrospheres) of ordinary and sweeper tentacles have characteristically different types of nematocysts, microbasic p-mastigophores, and large microbasic b-mastigophores, respectively (Hidaka and Yamazato, 1984). The acrosphere region of the squashed tentacle was scanned under a microscope and the number of each type of nematocyst was counted. When the acrosphere of a tentacle contained numerous microbasic p-mastigophores and no more than 20 large microbasic b-mastigophores, the tentacle was identified as ordinary tentacle. When the acrosphere of a tentacle contained numerous large microbasic b-mastigophores and no more than 20 microbasic p-mastigophores, the tentacle was classified as sweeper tentacle. When more than 20 of both microbasic p-mastigophores and large microbasic b-mastigophores were present in the acrosphere of a tentacle, the tentacle was classified as intermediate tentacle. In this experiment, the longest 20 tentacles that extended laterally were examined, though polyps usually have 30–50 tentacles. When the first 12 tentacles were revealed to be ordinary tentacles (this occurred only in histoincompatible pairs), the nematocyst composition of the remaining tentacles were not examined but they were assumed to be ordinary by external appearance alone.

After the examination of nematocyst composition, five pairs out of seven replicates were immersed in a 1:1 mixture of 10% formalin in sea water and 10% acetic acid to decalcify. After the completion of decalcification, the specimen was prodded lightly with forceps to examine whether the tissues of both polyps were continuous. The two remaining pairs were immersed in 5% commercial sodium hypochlorite solution to remove the soft tissue. The exposed skeletons were examined under a stereomicroscope to examine whether the skeletons were continuous or separated by a fine gap.

RESULTS

Nematocyst discharge responses

Colonies of *Galaxea fascicularis* were divided into several groups according to whether their ordinary tentacles discharged nematocysts against each other (Table I). Polyps did not discharge nematocysts against polyps of other colonies with the same or similar color. Polyps of a Wt or B colony did not discharge nematocysts against polyps of another Wt or B colony, respectively. There was an exception (Wt11–Wt12), although Wt11 is slightly different from other Wt colonies in that its

TABLE I

Nematocyst discharge responses between colonies of Galaxea fascicularis

A

Response	Stimulus								
	Wt11	Wt12	B13	B14	BG15	Gs16	Gs17	Gs18	Gs19
Wt11		+(3)	+(3)	+(3)	+(3)	+(3)	+(3)	+(3)	+(3)
Wt12	+(3)		+(9)	+(9)	+(3)	+(3)	+(3)	+(3)	+(3)
B13	+(3)	+(6)	-(9)	-(3)	+(9)	+(3)	+(3)	+(3)	+(3)
B14	+(3)	+(6)	-(3)		+(3)	+(9)	+(3)	+(3)	+(3)
BG15	+(3)	+(3)	+(9)	+(3)		-(9)	-(3)	-(3)	-(3)
Gs16	+(3)	+(3)	+(3)	+(9)	-(9)		-(3)	-(3)	-(3)
Gs17	+(3)	+(3)	+(3)	+(3)	-(3)	-(3)		-(9)	-(3)
Gs18	+(3)	+(3)	+(3)	+(3)	-(3)	-(3)	-(9)		-(3)
Gs19	+(3)	+(3)	+(3)	+(3)	-(3)	-(3)	-(3)	-(3)	

B

Response	Stimulus								
	Wt21	Wt22	B23	B24	B25	BG26	BG27	Gs28	Gt29
Wt21		-(3)	+(3)	+(3)	+(3)	+(3)	+(3)	+(3)	+(3)
Wt22	-(3)		+(9)	+(18)	+(3)	+(9)	+(3)	+(3)	+(3)
B23	-(3)	+(3)		-(9)	-(3)	+(9)	+(3)	+(3)	+(3)
B24	-(3)	+(1)	-(9)		-(3)	+(3)	+(3)	+(3)	+(3)
B25	-(3)	-(3)	-(3)	-(3)		+(3)	+(3)	+(3)	+(3)
BG26	+(3)	+(9)	+(9)	+(3)	+(3)		-(13)	-(13)	-(19)
BG27	+(3)	+(3)	+(3)	+(3)	+(3)	-(13)		-(13)	-(3)
Gs28	+(3)	+(3)	+(3)	+(3)	+(3)	-(13)	-(13)		-(14)
Gt29	+(3)	+(3)	+(3)	+(3)	+(3)	-(19)	-(8)	-(14)	

A and B show results of two series of experiments. +, Adhesion. -, Non-adhesion. Letters represent color morphs and numbers following the letters represent individual colonies. Tentacles of B morph colonies adhered only slightly to polyps of Wt morph colonies when it adhered. Number in parentheses indicates the number of tentacles examined.

tentacles on the major septa are whitish. Polyps of BG, Gs, and Gt colonies did not discharge nematocysts against each other, forming one group according to the present examination of the nematocyst discharge response. Colonies belonging to different groups discharged nematocysts against each other. In one combination of colonies (Wt-B), however, the nematocyst discharge appeared to be unidirectional. Polyps of B colonies failed to adhere or sometimes only weakly adhered to the target tissue of Wt colonies, while tentacles of Wt colonies strongly discharged nematocysts against the tissue of B colonies. Polyps of the same B colony discharged nematocysts normally against polyps of morphs other than Wt.

Contact experiments

When polyps isolated from colonies of different groups were paired, both of the paired polyps developed many sweeper tentacles (Table III). In some combinations,

TABLE II

Outcomes of the contact experiments between isolated polyps of Galaxea fascicularis

Source of the paired polyps	Nematocyst* discharge	Contact responses			
		Fusion	Filling	Aggression**	No contact and no response
Allogenic					
BG15-B13	+(9) +(9)	0	1	6 (BG15 > B13)	0
Wt22-BG26	+(9) +(9)	0	0	7 (Wt22 > BG26)	0
B14-Gs16	+(9) +(9)	0	7	0	0
B23-BG26	+(9) +(9)	0	3	0	4
Wt12-B13	+(9) +(6)/-(3)	0	0	7 (Wt12 > B13)	0
Wt12-B14	+(9) +(6)/-(3)	0	0	7 (Wt12 > B14)	0
Wt22-B23	+(9) +(3)/-(6)	0	0	5 (Wt22 > B23)	2
Wt22-B24	+(18) +(1)/-(17)	0	0	7 (Wt22 \cong B24)	0
Gt29-BG26	-(19) -(19)	0	6	0	1
Gt29-Gs28	-(14) -(14)	0	7	0	0
B23-B24	-(9) -(9)	0	6	0	1
Gs16-BG15	-(9) -(9)	7	0	0	0
Gs17-Gs18	-(9) -(9)	7	0	0	0
Syngenic					
B13-B13	-(9)	7	0	0	0

Seven replicated pairs were made in each combination of colonies and the number of pairs which fell into each category are shown. Letters indicate color morphs and numbers following the letters indicate individual colonies.

* +, Tentacle tips adhered to the opponent polyp. -, No adhesion was observed. Number in parentheses indicates the number of tentacles examined. Adhesion of tentacles of B morph colonies to polyps of Wt morph colonies was very weak when it occurred. The data are same as those shown in Table I.

** Aggression means that one of the paired polyps was damaged; the dominant polyps are on the left side of the inequality sign. Polyps of the Wt22 colony were dominant in four pairs and died in the other three pairs.

one of the paired polyps was damaged (aggression) (Table II; BG15-B13, Wt22-BG26). In other combinations, both polyps survived, without suffering any damage from the neighboring polyp, for five months (Table II; B14-Gs16, B23-BG26). Tissue fusion did not occur and a more or less vertical ridge was formed at the interface as a result of interfacial cementation (filling).

When polyps isolated from B and Wt colonies were paired, polyps of B colonies usually suffered damage from polyps of Wt colonies (Table II), though both of the paired polyps developed many sweeper tentacles (Table III). This indicates that polyps which discharge nematocysts against the opponent polyp are dominant over the polyps which do not, since it appeared that only polyps of a Wt colony discharged nematocysts against polyps of a B colony. In some cases, polyps from Wt colonies died in the early stage of the experiment (Table II; Wt22-B24). But this may be due to the fact that polyps of Wt colonies have shorter column wall tissue than polyps of other morphs and seem to be more sensitive to overgrowth by algae when isolated.

When polyps isolated from different colonies belonging to the same group were paired, filling or fusion occurred (Table II). In the former case, both polyps survived without suffering any damage from the neighboring polyp, but tissues of the paired

TABLE III

The number of ordinary, intermediate, and sweeper tentacles in the paired polyps of Galaxea fascicularis at the end of the contact experiment

Source of the paired polyps	Nematocyst* discharge	Number of tentacles (mean \pm S.D.)		
		Ordinary	Intermediate	Sweeper
Allogenic aggression				
BG15 > B13				
BG15	+	4.4 \pm 1.1 (7)	2.7 \pm 1.0 (7)	12.9 \pm 1.7 (7)
B13	+	0.5 \pm 0.8 (6)	1.2 \pm 1.6 (6)	13.8 \pm 3.9 (6)
Wt12 > B13				
Wt12	+	4.6 \pm 2.9 (7)	8.7 \pm 2.6 (7)	6.7 \pm 2.1 (7)
B13	+/-	1.7 \pm 2.1 (7)	2.7 \pm 1.5 (7)	13.1 \pm 3.2 (7)
Wt12 > B14				
Wt12	+	3.3 \pm 3.0 (7)	7.0 \pm 3.9 (7)	9.7 \pm 5.3 (7)
B14	+/-	6.2 \pm 2.8 (6)	2.2 \pm 1.2 (6)	10.5 \pm 3.3 (6)
filling				
B14-Gs16				
B14	+	3.0 \pm 2.8 (7)	1.1 \pm 1.2 (7)	13.6 \pm 3.8 (7)
Gs16	+	3.0 \pm 2.8 (7)	2.6 \pm 1.3 (7)	14.4 \pm 3.5 (7)
Gt29-Gs28				
Gt29	-	2.1 \pm 2.4 (7)	17.7 \pm 2.6 (7)	0.1 \pm 0.4 (7)
Gs28	-	9.4 \pm 7.2 (7)	10.4 \pm 7.4 (7)	0.1 \pm 0.4 (7)
Gt29-BG26				
Gt29	-	2.3 \pm 2.1 (7)	17.7 \pm 2.1 (7)	0 (7)
BG26	-	6.9 \pm 4.5 (7)	11.9 \pm 5.3 (7)	1.3 \pm 2.6 (7)
B23-B24				
B23	-	4.7 \pm 2.8 (7)	15.3 \pm 2.8 (7)	0 (7)
B24	-	18.3 \pm 1.3 (7)	1.6 \pm 1.1 (7)	0.1 \pm 0.4 (7)
fusion				
Gs16 = BG15				
Gs1	-	20 (7)	0 (7)	0 (7)
BG1	-	19.4 \pm 1.5 (7)	0.6 \pm 1.5 (7)	0 (7)
Gs17 = Gs18				
Gs17	-	20 (7)	0 (7)	0 (7)
Gs18	-	18.7 \pm 2.4 (7)	1.3 \pm 2.4 (7)	0 (7)
Syngenic fusion				
B13-B13				
B13	-	20 (14)	0 (14)	0 (14)

The number of the polyps whose tentacles were examined is shown in parentheses. Letters indicate color morphs and numbers following the letters indicate individual colonies. Inequality signs represent aggression; the dominant polyps are on the left side of the sign. Minus signs represent filling, and equality signs represent fusion.

* +, Tentacle tips adhered to the opponent polyp. -, No adhesion was observed. +/-, Weak adhesion was sometimes observed.

polyps did not fuse (Table II; Gt29-BG26, Gt29-Gs28, B23-B24). In this case a considerable number of intermediate tentacles were developed, though either polyp developed no or only a few sweeper tentacles (Table III; Gt29-BG26, Gt29-Gs28, B23-B24). In the latter case, tissues of the paired polyps fused with each other (Table II; Gs16-BG15, Gs17-Gs18). In this case both polyps possessed no sweeper tentacles and no or only a few intermediate tentacles (Table III; Gs16-BG15, Gs17-Gs18). Decalcified specimens did not separate into two pieces when prodded lightly,

indicating that the soft tissues are continuous. Examination of the skeletons also proved that the interface of the skeletons is smooth without an apparent gap between them.

When syngeneic polyps were paired, they fused and developed no sweeper or intermediate tentacles (Tables II and III) as previously reported (Hidaka and Yamazato, 1984).

DISCUSSION

The present results show that ordinary tentacles of *Galaxea fascicularis* play some role in self and non-self recognition. Colonies of *G. fascicularis* can be divided into groups according to whether their ordinary tentacles discharge nematocysts against each other. This is consistent with the previous study in which specimens of *G. fascicularis*, collected from another site, were used (Hidaka and Miyazaki, 1984). These groups corresponded to previously described color morphs, although color morphs Gs, Gt, and BG formed a group according to the present examination of nematocyst discharge response. Ordinary feeding tentacles must play some role in self and non-self recognition in sea anemones, since contact of feeding tentacles with nonclonemates can initiate aggression with acrorhagi or catch tentacles (Francis, 1973; Bigger, 1976; 1980; Lubbock, 1980; Purcell, 1977).

When two polyps that discharged nematocysts against each other were paired, both polyps developed many sweeper tentacles. When two polyps that did not discharge nematocysts against each other were paired, neither polyp developed sweeper tentacles. This indicates that the nematocyst discharge response of ordinary tentacles is important in eliciting formation of sweeper tentacles. Chornesky (1983) reported that, in *Agaricia agaricites*, sweeper tentacle formation can be elicited also by contact with tentacle tips of other corals. This may also indicate that nematocyst discharge plays an important role in eliciting sweeper tentacle formation. However, incompatible polyps developed many intermediate tentacles when kept in contact, even if they did not discharge nematocysts against each other. This suggests that the histoincompatibility response may also stimulate formation of sweeper tentacles though at a slower rate.

An alternative interpretation is that both nematocyst discharge and sweeper tentacle formation are elicited when the degree of histoincompatibility exceeds a certain limit and that nematocyst discharge is not necessarily involved in eliciting sweeper tentacle formation. A further study might be necessary to exclude this possibility.

When two polyps that do not discharge nematocysts against each other but which were isolated from different colonies were paired, the tissues of the paired polyps sometimes fused and at other times did not fuse. This indicates that polyps sometimes recognize polyps from other colonies as non-self at the level of histoincompatibility response, even when the ordinary tentacles do not discharge nematocysts against them. This indicates that self and non-self is more finely recognized in the histoincompatibility response than in the nematocyst discharge response, and is consistent with the previous results with *Pocillopora damicornis* (Hidaka, in prep.). It is not clear whether fused polyps were derived from syngeneic colonies produced by asexual reproduction such as fragmentation. It was suggested that colonies of *G. fascicularis* may reproduce asexually by fragmentation in addition to sexual reproduction (Hidaka and Yamazato, 1982). It is also possible that allogeneic polyps can fuse with each other when genetic difference is very small, contrary to the "uniqueness of the individual principle" proposed by Hildemann *et al.*, (1977a,

1980). Recently, Willis and Ayre (1985) observed one fusion of electrophoretically different colonies of *Pavona cactus*.

It is interesting that some pairs survived for five months without suffering any damage from the neighboring polyp even though both polyps had developed many sweeper tentacles. It is probable that some process of habituation occurs and allows allogeneic polyps to survive side by side without suffering any damage. Such a habituation process may occur in the sea anemones *Metridium senile* (Purcell and Kitting, 1982) and *Anthopleura xanthogrammica* (Sebens, 1984). Purcell and Kitting (1982) suggested that habituation is a major factor that allows different clones of sea anemones to live intermingled with each other without interclonal aggression.

The present results strongly suggest that the nematocyst discharge response has an important role in eliciting formation of sweeper tentacles and that self and non-self are more finely recognized in the histoincompatibility reaction than in the nematocyst discharge response.

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